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ABSTRACT

These materials were designed to be used by life science students for instruction in the application of physical theory to ecosystem operation. Most modules contain computer programs which are built around a particular application of a physical process. Thermoregulation is defined as the ability of an organism to modify its body temperature. This module emphasizes animal thermoregulation from an ecological point of view and develops the concept of the operative environmental temperature, a technique which integrates the effects of all heat transfer processes into one number. Historical developments in the study of animal thermoregulation are reviewed and an attempt is made to illustrate how a quantitative knowledge of heat transfer processes can be used to clarify the adaptive significance of animal morphology, behavior, and physiology. A problem set illustrates and extends ideas developed in the text. (Author/CS)

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SE 033 590

ANIMAL THERMOREGULATION AND THE OPERATIVE ENVIRONMENTAL (EQUIVALENT) TEMPERATURE

by

R.D. Stevenson

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June 1979

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PREFACE

The biological aspects of thermoregulation are investigated in this module by illustrating the limitations of purely physical models of heat balance. The importance of certain behavioral physiological and morphological traits is stressed throughout the discussions. A recent concept in the ecological literature, "the operative environmental temperature," is presented and discussed as a means of incorporating the relative influences of all heat transfer processes into one number. The upper division and graduate level college students interested in physiological ecology will find this module of interest. For maximum benefit, the accompanying problem set should be worked.

TABLE OF CONTENTS

	Page
PREFACE	ii
INTRODUCTION	1
ANIMAL THERMOREGULATION	1
The Physical Environment	4
Thermoregulation and the Ecogeographical Rules	10
Other Ecological Considerations	16
THE OPERATIVE ENVIRONMENTAL TEMPERATURE	19
Mathematical Development of the Operative Environmental Temperature	20
Laboratory and Field Applications of the Operative Environmental Temperature	24
Field Applications	29
SUMMARY	31
LITERATURE CITED	34
PROBLEMS	42
PROBLEM SOLUTIONS	48
APPENDIX I	56

INTRODUCTION

Whereas previous modules dealing with heat energy have introduced physical principles (Gates and Stevenson 1978; Stevenson 1977a,b, 1978a) or methods of analysis (Hatheway 1978, Stevenson 1978b), the first section of this paper will emphasize animal thermoregulation from an ecological viewpoint. Physiologists have investigated thermoregulation more than ecologists so the student will find the best summaries in environmental physiology texts such as Gordon (1977) and Schmidt-Nielsen (1975) or summary reviews (Whittow 1970, 1971, 1973; Precht et al. 1973; Wieser 1973). Gibbons and Sharitz (1974) and Gates and Schmerl (1975) also contain papers which are of interest to students of thermal biology. The material within is meant to complement these standard treatments. Even though all the examples are of animals, one can also think of plants as thermoregulating. Plants modify leaf shape, position and surface characteristics as well as daily and seasonal photosynthetic periods. The last part of the module develops the concept of the operative environmental temperature, which we will see is a useful way to integrate the effects of all heat transfer processes.

ANIMAL THERMOREGULATION

The term thermoregulation can be defined as the ability of an organism to modify its body temperature. Although this may seem simplistic, the point is that a living organism often has a body temperature which would be different from that of an inanimate object with the same physical properties as the organism in the same thermal environment. For endothermic organisms, this fact is well known. The constancy of internal temperature of these animals helped Claude Bernard, a century ago, form his opinion that homeostatis is the central paradigm of physiology. But it was not until

Heath's (1964) paper that this point was clearly made for ectotherms. Huey (1974) studied the time and energy costs of regulating body temperature by contrasting body temperatures and spatial and temporal distributions of an iguanid lizard, Anolis cristatellis, in two different adjacent thermal environments--an open park and a forest. This ecological viewpoint is given a more general treatment by Huey and Slatkin (1976) in which they consider the costs and benefits of thermoregulation. Biologists have always recognized that the consequences of altering body temperature are profound. Today more emphasis is being placed on interpreting the importance of thermoregulation for circadien rhythms, circannual rhythms, foraging and digestive processes of individuals in their natural environment.

One can begin to understand the costs and benefits of temperature regulation by outlining the mechanisms that allow an organism to thermoregulate. In Table I, these are placed under three convenient headings: behavioral, physiological and morphological. This breakdown also chosen by King (1974) and West (1977) provides a starting point for discussion of alternative thermoregulation strategies. One might begin by determining the relative importance for influencing heat transfer of each mechanism and its energetic cost to the organism. This kind of information is generally not known, but we will discuss one example later in the text which contrasts the effects of increasing body size and insulation thickness on heat loss.

What kinds of information are available from Table 1? First, the time scale on which each mechanism operates gives clues about the kind of environmental changes for which the mechanism has evolved to compensate. Second, the physical environment may dictate that certain mechanisms cannot be used. One obvious example is that of evaporative cooling in dry environments (Schmidt-Nielsen 1964). Here an organism must find other means to

TABLE 1. Systems or Mechanisms Influencing Thermoregulation in Animals

Behavioral	Time Scale of Adjustment
Habitat selection	S,L
Temporal selection of microhabitat	M,D
Spatial selection of microhabitat	M,D,S
Orientation	M
Body	
Body appendages	
Caloric intake	D,S
Piloerection	M
Intraspecific grouping	M,S,L
Physiological	
Metabolic rate	M,S
Blood flow rate	M
Water loss	M
Respiratory	
Panting	
Sweating	
Cutaneous	M
Color	S
Fat distribution	S
Fat melting point	
Morphology	
Color	S
Size	L
Shape	L
Surface characteristics	S
Fur	
Feathers	
Scales	
Circulatory system	L
Counter current exchanges	L
Shunts	L

M = Minute
D = Day
S = Season
L = Lifetime

reduce its heat load because water is in short supply and is required for other purposes. A further complication is the interaction of several mechanisms. Consider the example of metabolic output as a function of air temperature given in most physiological texts. As the air temperature is lowered, the animal can maintain a thermal equilibrium by simply restricting blood flow to peripheral areas (vasoconstriction). This reduces the temperature in these areas (see Fig. 1a). At the end of the thermal neutral zone when all the vessels are constricted (hot-cold dividing line in Fig. 1b), the organism must increase its metabolic rate if its body temperature is to remain constant. In contrast, the blood vessels of an active animal must be dilated to supply the muscles with oxygen. Metabolic rate may increase by 300% or more to provide the energy for activity. Figure 2 shows resting and active metabolic rates for the rabbit Oryctolagus cuniculus as a function of temperature. When the rabbit is active, the metabolic rate is independent of air temperature. The challenge of physiological ecologists is to understand these mechanisms and their interactions for the animal in the natural environment.

The Physical Environment

Another approach for studying thermoregulation is to examine the temporal and spatial variation of the thermal environment. This variation is a result of the patchiness and gradients of the physical factors in the heat energy equation: solar radiation, longwave radiation, wind speed, wind direction, air temperature, substrate temperature and water vapor concentration or water temperature. Vertical temperature gradients formed in the water, soil or air may allow an organism to locate in its preferred thermal environment. The increase in wind speed above the ground surface forms

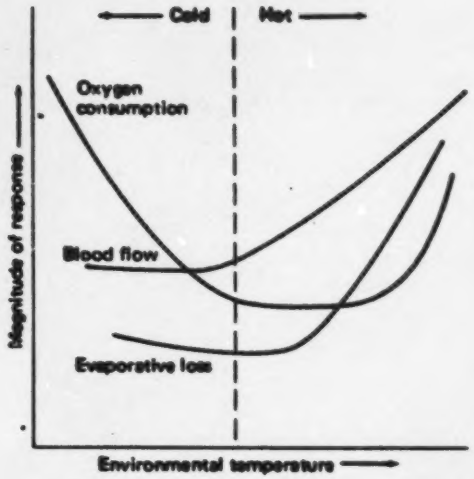

Figure 1a. Oxygen consumption curve for a hypothetical homeotherm. The terms "hot and "cold" can be defined in terms of the animal's physiological responses to its environmental temperature. (From Ingram and Mount 1975, p.2.)

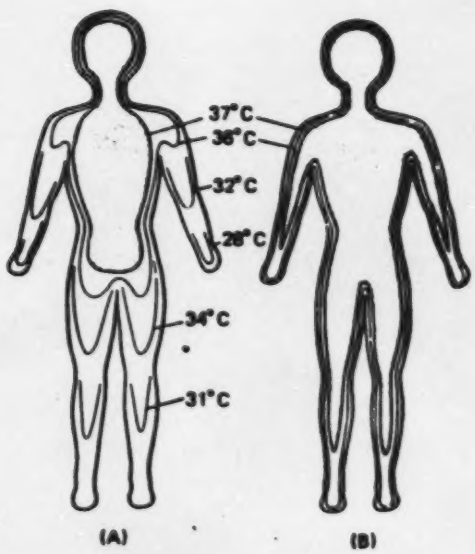

Figure 1b. Diagrammatic isotherms in the human body exposed to cold (A) and warm (B) conditions. The core of deep body temperature (shaded) shrinks in the cold, leaving a peripheral shell of cooler tissue. (From Ingram and Mount 1975, p. 6: original data from Aschoff and Wever 1958.)

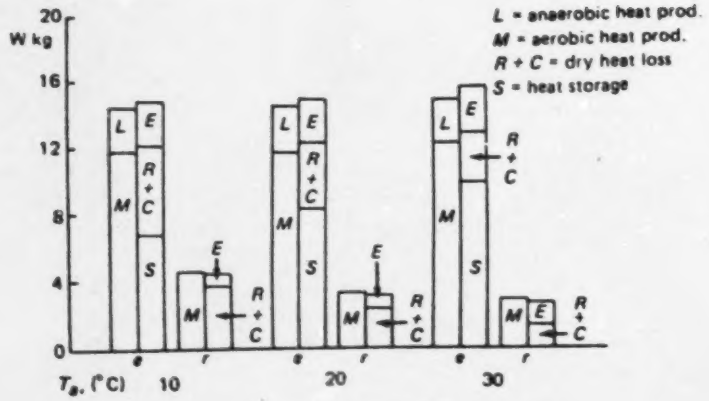

Figure 2. Mean heat production, loss and storage in three exercising (c) and four resting (r) New Zealand white rabbits at ambient temperatures of 10, 20 and 30°C. (From Kluger et al. 1972a.)

another kind of gradient. Patches usually created by sun and wind shadows are the result of the landscape and vegetation. If the patches are large compared to the size of the organism, then it may be necessary for the organism to move between patches to remain in thermal comfort. Hillman (1969) describes this behavior for the lizard Amevia leptophrys, which makes excursions into the forest habitat to forage but returns to the shrub community where sunlight is available to increase its body temperature. If patches are small, it may be possible for the animal to "sit" in two or more different thermal environments so as to balance its thermal energy exchange. If the patches become very small relative to the organism, the environment will appear homogeneous.

Another characteristic of the physical environment is that under certain conditions (e.g., clear or uniformly cloudy sky), the variability of thermal patches can be characterized quantitatively. Thus one can predict how the thermal environment will change in time and space. The work of Porter et al. (1973), who studied the desert iguana Dipsosauros dorsalis, is the best example of this modeling approach.

The reader should realize that the larger the variability in the micrometerological conditions the greater is the thermal stress the organism potentially experiences. In fact, most research has concentrated on adaptations to stressful environments. Physiologists have studied heat stress in deserts and cold stress in polar regions. This is the most likely course of investigation because the environments are harsh and the evolutionary solutions intriguing. Simple reasoning, however, suggests that a more complex viewpoint will have to be adopted for a complete understanding of animal thermoregulation in an ecological context.

Consider an arctic fox in the cold winter of the northern tundra. With a deep body or core temperature of about 38°C, it will be losing heat energy to the environment. Why is it that the fox does not increase its passive insulation (fur thickness) to conserve energy? One answer is that the animal would quickly overheat if its fur were too thick when it was exercising. This would have profound implications for the fox's ability to capture prey. Bartholomew and Wilke (1956) and Brown and Lasewski (1972) provide examples relevant to this point.

Remember also it is probable that an animal can be too hot in the arctic winter and it may also become too cold in the tropics. It is likely that on any given day within any habitat an organism can experience either extreme. Thus the diversity of mechanisms found in Table 1 is not so surprising. Animals have a complex integrated approach for regulating their internal environment.

Finally note that an organism has two ways of dealing with thermal stress. It can tolerate the variability through physiological adaptations or it can avoid these climates or microclimates. The antelope ground squirrel Citellus leucurus, as most animals, employs both of these means. This desert mammal has evolved a large tolerance for body temperature fluctuations so that it can be active during the day under intense solar radiation. These conditions impose a net gain in heat energy and a corresponding rise in body temperature. To avoid thermal stress, the animal must retreat to its burrow where it can lose energy to the surrounding soil. Figure 3 shows the expected time course of its body temperature. When the body temperature drops, the animal has retreated to its burrow. We conclude that C. leucurus uses a combined strategy of tolerance and avoidance to be active on the sunlit desert surface.

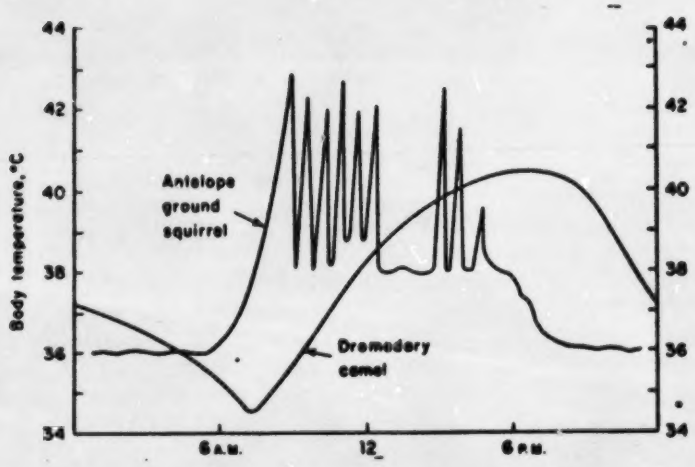

Figure 3. Diagrammatic representation of the daily patterns of body temperatures in a large and a small mammal subjected to heat stress under desert conditions. (From G.A. Bartholomew 1977, p. 423; original data from Schimdt-Nielsen et al., 1957, Amer. J. Physiol. 188: 103-112, and J.W. Hudson, 1962, Univ. Calif. (Berkeley and Los Angeles) Publ. Zool. 64:1-56.

Thermoregulation and the Ecogeographical Rules

During the coures of their studies, early natural historians noted that there were clines in homeotherm size, shape and color. Three empirical ecological rules bearing the names of Bergmann, Allen and Gloger resulted from these observations. In addition, Cowles (1946) observed that there was a decrease in lizard body size at increasing latitudes. In each case, the originator proposed a reason why these observations might be true based on the animal's thermal relation to the environment. The knowledge of energy balance and heat transfer processes explained in earlier modules (Stevenson 1977a,b, 1978a) will prove to be especially helpful in clarifying and dissecting each hypothesis.

Bergmann (1847) originally observed that, as the environment became colder, mammal and bird size increased. Although Mayr (1963, p. 323) has restricted Bergmann's rule to variation within races, James' (1970) translations indicate that Bergmann intended his rule to apply to larger taxonomic groups. To explain his generalization, Bergmann proposed that increasing body size would reduce heat loss. He reasoned that, since heat loss is proportional to surface area, metabolic output should be proportional to body mass to the .67 power. Increasing body size would therefore decrease the metabolic output per unit body weight.

There are several objections to this line of reasoning. First, modern measurements of standard metabolic rates of homeotherms have shown that resting metabolism is not proportional to the mass to the 0.67 power, but rather the 0.75 power. (Readers should consult McMahon (1973) for a suggestion of why this might be true.) Second, in a classical paper, in which they compared tropical and arctic birds and mamals, Scholander et al. (1950a) found that in most cases standard metabolism is independent of the

environment. Challenging the physiological basis of Bergmann's rule in a later paper, Scholander (1955) stated that there were three ways in which an organism could adapt to a colder climate: (1) by lowering the thermal gradient (decreasing body temperature), (2) by increasing metabolic rate or (3) by increasing body insulation. Based on earlier work (Scholander et al. (1950b,c)), Scholander (1955) concluded that homeotherms increase fur and feather thickness to endure the colder climate of the arctic. This paper spurred a series of comments and rebuttals (Mayr 1956, Newman 1956, Irving 1957, Scholander 1956) which mainly serve to point out that there is a difference between the empirical observation and the reason for the "law." As McNab (1971) correctly points out, a third objection is that increasing body size would reduce the heat loss per unit surface area, but in fact the total heat loss would increase as $M_b^{0.25}$. Increasing body size requires absolutely more energy. McNab concluded that much of the data used to support Bergmann's rule could be interpreted as classical examples of character displacement (Brown and Wilson 1956).

These three arguments provide evidence to dismiss Bergmann's reasoning. The empirical basis of Bergmann's rule, however, is still supported by more careful recent studies (James 1970, Brown and Lee 1969). The question now becomes "What selective forces would favor increasing body size in colder environments?"

Kendeigh (1969) made the plausible suggestion, for birds at least, that increasing body size will allow the animals to survive the critical times of severe weather when feeding is impossible. Developing this argument more formally, Calder (1974) states that during such conditions when the birds cannot forage, survival time depends on the amount of fat that is stored which is proportional to body mass. Because metabolism is proportional to

$M_b^{.75}$, a larger bird can survive a proportionately longer time. Ketterson and Nolan (1976) discuss this hypothesis in relation to body size and the sex clines they found for the Dark-eyed Juncos, Juncos hyemalis hyemalis. The ecologist, however, is still left to explain McNab's objection that a larger animal needs absolutely more energy. This might be rephrased as "Can a bird slightly larger than its conspecifics forage at a proportionately greater rate to meet its larger energy requirements?"

Spotila and Gates (1975) provide the only study that addresses Bergmann's role and specifically incorporates the heat transfer processes. They conclude that indeed increasing body size will decrease the metabolic rate per unit surface area to achieve thermal equilibrium. Figure 4 clearly shows that size acts as insulation reducing the metabolic output. Given the alternative of increasing size or adding insulation, though, Figs. 4a and b show that a homeotherm (T=42°C) 2 cm in diameter in a cold environment can get the same reduction in metabolism by increasing insulation thickness 10 times instead of increasing body size to 10 cm in diameter. Their model only investigated the steady state situation. It would be instructive to incorporate temporal variations in the thermal environment.

In 1877, Allen wrote that species from colder climates often have smaller appendages than do closely related species in warmer climates. He suggested that this was an adaptation to conserve heat in cold environments. Mayr (1963) states that Rensch (1933) made quantitative measurements which upheld Allen's rule. The problem is that decreasing surface area decreases the rate at which an organism can absorb energy as well as release energy. If the environment if always colder than the organism, it should assume a spherical shape and avoid the plate shape. As already noted earlier in the text, at times it may be important to increase heat loss even in the coldest

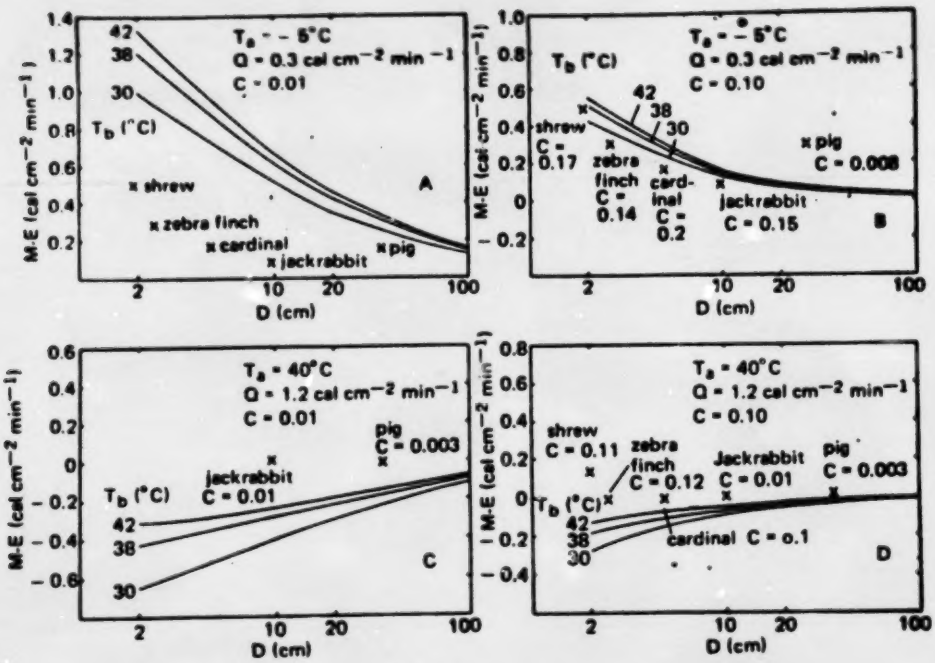

Figure 4. Effect of body size and insulation on the M-E requirement of homeotherms. (A) Cold conditions, clear sky at night, low insulation. (B) Cold conditions, clear sky at night, increased insulation. (C) Full sun, high air temperature, low insulation. (D) Full sun, high air temperature, increased insulation. Insulation consists of a layer of fur or feathers, the thickness of the layer defined as C·D, where D is the inside diameter with no insulation and C is a constant proportion of D for all sizes of D in a given set. Data for real animals are taken from Porter and Gates (1969). (From Spotila and Gates 1975, p. 295.)

environment. By reducing surface area, the organism has less ability to direct blood flow to influence its heat balance physiologically, but an increase in the surface area to volume ratio may require more energy to keep surface tissue from freezing. The effects of natural selection on such trade-offs are not clear.

There are several well-documented examples of the importance of appendages in thermoregulation. Farlow et al. (1976) investigated the sail fin of the dinosaur Stegosaurus. Studies of the vascular system and a model of heat transfer implicate the dorsal fin as an important heat transfer mechanism. The pinna of Leporidae (hares and rabbits) is a favorite topic of vertebrate physiologists (Kluger et al. 1971, Hill and Veght 1976, Schmidt-Nielsen et al. 1965,Wathen et al. 1971). These investigators have shown that the large surface area (20% of the body) of the external ear is a useful mechanism to control heat exchange. Their large surface area, which improves convective and radiation exchange, combined with the ability to pump blood through the tissue makes an effective regulation system. Wathen et al. (1971) have made wind tunnel and theoretical investigations exploring various geometrics. Hesse (1928) and Griffing (1974) provide empirical evidence for Allen's rule. But there are no theoretical studies comparable to the work of Spotila and Gates (1975) to help interpret this phenomenon.

Gloger (1833) postulated that lighter colored animals are found in more open habitats because they emitted more radiation. From modern physics, however, we know that color is not important in determining emissivity to longwave radiation. Almost all organisms have emissivities above 0.5 (Monteith 1973). Hock (1965) pointed this out and ascribed the importance of color to camouflage. In his investigation of animal color, Hamilton (1972) distinguishes three categories: communication, camouflage (from

predators and from prey) and radiation exchange. He correctly states that color will be important for absorption of solar radiation. Hamilton (1972) believes that open habitat birds often have the problem of overheating in the daytime. In this environment, coloration will reflect solar radiation thus reducing the heat load. Since these habitats also tend to be cooler at night, these birds should have thicker plumage to conserve heat after dark. Hamilton presents some comparative and physiological data which supports his hypothesis. Ohmart and Lasiewski (1970) and Lustick (1969) have made O_2 consumption measurements below the thermal neutral zone showing that black-colored birds have reduced metabolic requirements compared to white birds. If the reader understands radiation transfer, this result is not so surprising. In fact, the reduction in metabolic rate can be accurately predicted as shown later in the module.

The heat transfer processes in the fur and feathers are just beginning to be explored (Davis and Birkeback 1974, Cena and Monteith 1975a, b,c). Physically, as light penetrates the pelage or plumage, it gets reflected forward and backward creating concave temperature distributions. Kowalski (1978) has found the radiation and conduction processes are coupled in the heat transfer. In general, a white-colored outer layer will absorb less radiation, but as wind speed increases, Walsberg et al. (1979) found that the reduction in absorbed radiation for black feathers was larger. This is because the maximum temperature in the plumage layer was closer to the surface in the black than in the white feathered skin. Therefore convection will have a larger effect on the black-colored bird. Further studies will be able to investigate fur and feather characteristics (thickness, length, density) which eventually can be incorporated into a model of the total animal in the environment to understand the interactions of wind speed and

radiation on absorbed radiation.

In 1946, Cowles suggested that lizard size should decrease with increasing latitude because increasing size would decrease the rate at which a reptile could achieve activity temperature. This hypothesis has never been rigorously tested. Ray (1960) and Lindsay (1966) examined latitudinal trends in size changes for a variety of invertebrate species but reached no conclusions.

Most models of thermoregulation have started with certain assumptions about the morphology and physiology of the organism and then attempted to ask about the control of body temperature (Huey and Slatkin 1976) or the limit of activity times (Belovsky 1977; Porter et al. 1973, Porter and Tracy 1975) and habitat (Tracy 1976). Other characteristics such as body shape and size, surface characteristics (scales, hair, feathers), preferred body temperatures, basal metabolic rate, and the design of the circulatory system also merit our attention since they too are under selective pressures. For instance, a question of interest for many years has been the evolution of homeothermy (Cowles 1946, Ricgles 1974, Whittow 1973, Heath 1968, Bakken 1971, Bakken and Gates 1975, Heinrich 1977, McNab 1978, Stevens 1973, Dawson 1975, Bouvier 1977, Calloway 1976, Crompton et al. 1978, Hainsworth and Wolf 1978). The question of preferred body temperature obviously has implications for the biochemical system of the organism which is also being investigated (Brock 1967, Hochaka and Somero 1973, Somero and Low 1975).

Other Ecological Considerations

Because of its very existence, every organism exchanges heat energy with its environment, it is natural to ask about the relation of thermoregulation to the tasks an individual must perform which include growth,

procurement of food, avoidance of predation and reproduction. Although these are standard subjects for ecological studies, their relation to thermoregulation is largely unexplored. Several paragraphs on the interaction of feeding and temperature regulation are included to spur the reader's interest.

It seems quite natural that the ecologists studying thermoregulation should become interested in the food requirement of their subjects. The chemical energy obtained is used for basal metabolism as well as all other tasks the animal must perform. In turn, the metabolic rate is a significant component of the heat energy balance of homeotherms, while for poikilotherms the thermal environment will influence the animal's body temperature and thus its metabolic rate.

What about ecologists interested in predicting an animal's food items? Investigators modeling feeding strategies (although not specifically concerned with thermoregulation costs) have provided some insight into temporal patterns and foraging modes (see Pyke et al. 1977 and Norberg 1977). Schoener (1974) states that an organism should forage during a given period if the energetic gain is greater than resting during that period. Symbolically this is stated: The animal shall forage if

$$e_x > -W_x \qquad (1)$$

where

e_x is the net energy gained while feeding in a period of type x

W_x is the energy lost while waiting through a period of type x.

He summarizes:

> These considerations imply that temporal specialization should vary with food abundance in exactly the opposite manner to food or habitat specialization. In situations of very high

> food abundance, only the best item kind is taken and only the best patch type is foraged in. Hence specialization on food type and habitat is at its maximum, But under situations of greatest food abundance, there should be no time during which feeding results in a greater loss of energy than waiting. Hence temporal specialization is at its minimum. With decreasing food abundance, item kinds and habitat types are added, but it is possible that food availability becomes so low during certain periods of time that it is less expensive to wait those periods out. Hence food and habitat type broaden while diet activity periods shrink as abundance decreases.
>
> ... Of course it is possible that animals will not be as generalized with respect to time as contingency models imply, if by being so generalized they gain more food than they can process. Such animals, or any animal with a fixed caloric requirement should specialize with respect to time as food abundance increases, just as they should for food or habitat. Thus contingency feeders and restricted feeders should react in opposite ways to changes in overall food abundance. Williams (10) reports that during poor weather when yield from the best feeding periods is less, certain animals (daddy-longlegs, cattle) enlarge their activity times. Such animals are behaving as if they have a fixed caloric quota.

It is instructive to separate the net energy gained during a period x into the food ingested and the metabolic costs of foraging in that environment. Often the foraging environment is thermodynamically different from the resting place. Feeding also means a concomitant increase in metabolic rate. Bearing these facts in mind, equation 1 can be expanded into the following form:

$$F_x - M_{fx} > M_{rx}$$

where

F_x is energy captured (W),

M_{fx} is metabolism while foraging (W),

and M_{rx} is metabolism while resting (W).

If the costs of the two environments are much different or the probability of finding food is low, it may be that an organism should skip foraging periods more often. Consideration of the daily and seasonal foraging patterns of organisms suggests the question: "Why do animals spend so much of their time waiting or resting?" Katz (1974) developed a long-term foraging optimization scheme to investigate some of these issues. Brett (1971) provides some intriguing data on the interaction of food levels and temperature.

The remainder of this module returns to questions of heat balance. The ecologist, however, must constantly keep this broader perspective in mind if he or she is to investigate the patterns found in nature.

THE OPERATIVE ENVIRONMENTAL TEMPERATURE

Models of the physical processes that govern the heat energy exchange of animals involve many environmental as well as organismal parameters which make the results difficult to summarize. One must use the four heat transfer processes, radiation, convection, evaporation and conduction to link the microclimate (air temperature, wind speed, etc.) to the animal's physiology, behavior and morphology. With such a large number of independent variables, it is apparent that it would be helpful to have a single number that would allow one to say how the animal "felt" in that environment. At first this may seem difficult. For example, if all the environmental variables and homeotherm's thermoregulatory actions are fixed, the organism will have a specific metabolic rate. It is possible, however, to change the external conditions--say reduce the body-air temperature difference but increase the wind speed so that the organism will have the same metabolic rate to maintain

thermal equilibrium or one could lower the air temperature but increase the absorbed radiation so that a poikilotherm would not have a different body temperature. The concept of operative environmental temperature lets one say quantitatively which environments are equivalent thermodynamically for the organism. Because this concept undercuts the physical processes, valuable information is lost about the animal's coupling to the environment. But indeed this is the purpose of the operative environmental temperature. It may actually be that animals respond to a stimulus that has already integrated all the thermal fluxes.

Mathematical Development of the Operative Environmental Temperature

In this section, I develop the operative environmental temperature (T_e) as Bakken and Gates (1975) presented it. Other authors have described something closely akin or exactly equivalent to T_e, but I find the following derivation to be the most straightforward. A discussion and summary of alternative formulations can be found in Bakken (1979a) about which I will comment briefly later.

I will begin with a simple model that approximates a homeotherm. The heat transfer processes and heat sources included are absorbed radiation, reradiation, convection, respiratory and cutaneous water loss and metabolism. Applying the First Law of Thermodynamics to the surface of the animal at temperature T_r shows that

Energy In = Energy Out

and thus

$$Q_a + K(T_b - T_r) = Q_e + C + E_r \qquad (3)$$

where

Q_a = absorbed radiation ($W\ m^{-2}$)

Q_e = reradiation ($W\ m^{-2}$)

= $\sigma\varepsilon T_r^4$ (σ is Stefan-Boltzmann's constant 5.67×10^{-8} $W\ m^{-2}\ K^{-4}$ and ε is emissivity),

and C = convection ($W\ m^{-2}$)

= $h_c(T_r - T_a)$ (h_c is the heat transfer coefficient of convection ($W\ m^{-2}\ °C^{-1}$) and T_a is air temperature (°C)),

$K(T_b - T_r)$ = the heat flowing from the isothermal core at temperature T_r °C where K is the thermal conductivity of the body ($w\ m^{-2}\ °C^{-1}$),

and E_r = that water loss at the skin times the latent heat of evaporation ($W\ m^{-2}$).

Similarly, within the body

Energy In = Energy Out

$$M = E_b + K(T_b - T_r) \tag{4}$$

where

M = the metabolic rate ($W\ m^{-2}$),

and E_b = water lost during respiration mutliplied times the latent heat of evaporation ($W\ m^{-2}$).

These two equations will govern the steady state behavior of our system. The fourth power of the reradiation term complicates solving for body temperature. To facilitate the solution, Bakken and Gates (1975) used a Taylor series expansion of two terms to approximate reradiation. In general, the Taylor series is

$$f(x) = f(\bar{x}) + f'(\bar{x})(x-\bar{x}) + f''(x-\bar{x})^2 + \ldots + f^n(x-\bar{x})^n + \ldots \quad .$$

If we expand about the mean surface temperature $\bar{T}_r$, then

$$T_r^4 \simeq \bar{T}_r^4 + 4\bar{T}_r^3(T_r-\bar{T}_r) = (4\bar{T}_r^3)T_r - 3\bar{T}_r^4 \quad .$$

The reradiation term is

$$\sigma\varepsilon\, T_r^4 \simeq (4\sigma\,\varepsilon\,\bar{T}_r^3)T_r - 3\sigma\varepsilon\,\bar{T}_r^4 \quad .$$

For convenience, we follow Bakken and Gates (1975) and let $4\sigma\varepsilon\,\bar{T}_r^3 = R$ and define $Q_n = Q_a + 3\sigma\varepsilon\,T_r^4$. Equation 3 can then be rewritten as

$$Q_n + K(T_b-T_r) = R\,T_r + h_c(T_r-T_a) + E_r \quad . \tag{5}$$

Equations 4 and 5 are then solved simultaneously to eliminate the surface temperature T_r. The rationale for this manipulation is the one not really concerned with the surface temperature. The question is "How are the animal's body temperature and physiological processes being influenced by the thermal environment?" Completing the elimination yields

$$T_b = \frac{h_c\,T_a + Q_n}{R + h_c} + (M-E_b)\,\frac{K + h_c + R}{h_c + R} - \frac{E_r}{R + h_c} \quad . \tag{6}$$

The important point of equation 6 is that the first term of the right-hand side does not depend on any physiological processes. It measures the component of the body temperature that is strictly due to the physical environment. This is the term Bakken and Gates (1975) labeled the operative environmental temperature, T_e. They say

> T_e may be identified as the temperature of an inanimate object of zero heat capacity with the same size, shape

> and radiative properties as the animal and exposed to the same microclimate. It is also equivalent to the temperature of a blackbody cavity producing the same thermal load on the animal as the actual non-blackbody microclimate, and therefore may be regarded as the true environmental temperature seen by that animal.

Bakken (1976a,b) and Bakken and Gates (1975) have extended these ideas in several ways. Most importantly they show that more complicated models including conduction can be incorporated into this same framework. Second, as Bakken (1976a) notes, the operative environmental temperature strictly speaking is not a temperature. This is because two systems are said to have the same temperature if each is in thermal equilibrium with a third system (Stevenson 1977a, Zemansky and Van Ness 1966). If the animals were of different size, the convection coefficient would be different and the two T_e's would not be equal. Yet each model organism would be in thermal equilibrium with the microclimate but not each other. Therefore, the zeroth law is not satisfied. This, however, is not a drawback for the use of T_e in temperature regulation studies.

Bakken (1976a), following Gagge (1940), has made the further complication of introducing the standard operative environment temperature. He felt this step was necessary so that the primary physiological response of animals to their thermal environment (metabolic rate minus evaporative water loss) could be unambiguously defined in a metabolic chamber. Although it was the purported intention of the operative environmental temperature to incorporate all the effects of the thermal environment into one stress index, the standard operative environmental temperature was created because the overall heat transfer coefficient between the animal and the environment (see K_o, p. 21) must uniquely define for the effective dry heat production to be predicted. The overall conductance depends on wind speed and the

thermal properties of the underlying substrate which can be standardized in metabolic chambers. The approach has the advantage of being able to relate laboratory experiments to field studies as well as decreasing the differences environmental temperature are found in Bakken (1976a, pp. 357-367).

Unfortunately, like the operative environmental temperature, this concept has limitations which Bakken (1976a) discusses. In particular, it is assumed that body temperature, posture, orientation and blood flow rates are constant. This is not necessarily the case. Simply the stress state of the animal may increase metabolic rates. Furthermore, this formulation does not account for the differences in water loss rates due to effects of changing ambient water vapor concentration (see Bakken 1979a for references including this effect). A forthcoming example, however, indicates that the standard operative environmental temperature can be useful.

One final comment is necessary before preceding. Bakken and Gates (1975) approximated the heat transfer between the animal and environment by linearizing about the mean surface temperature. Robinson et al. (1976) gave two derivations linearizing about air temperature and about the operative environmental temperature. Bakken (1979a) has evaluated the errors in these different approaches and finds that only in the case of naked animals do any of the alternatives give poor results. He further presents a procedure using numerical techniques to get exact results which is important for calculations of the heat balance of naked animals or in simulation studies where errors can accumulate.

Laboratory and Field Applications of the Operative Environmental Temperature

For many years, standard metabolic output has been measured as a function of air temperature. If the environmental chamber is large, the air

temperature will closely approximate the T_e, but small chambers can introduce error (Morhardt and Gates 1974, Porter 1969). In the natural environment, organisms experience a variety of shortwave radiation levels. But if T_e for different environmental combinations is the same then one would expect the same metabolic output for homeotherm or body temperature for a poikilotherm. To test this, Mahoney and King (1977) recently completed these calculations from De Jong's (1976) experiments. Their results are shown in Fig. 5. The metabolic output of White Crown sparrows, Zonorichia leucophrys gambelii, corresponds closely to the predicted values. Mahoney and King (1977) also performed some laboratory preference tests using different combinations of absorbed radiation and air temperature to obtain a range of operative environmental temperatures. Their results are expressed as cumulative time spent in each microhabitat (Fig. 6). Comparing Figs. 5 and 6 shows that the animals actually preferred to be in an environment near the lower end of their thermoneutral zone. It would be interesting to know how active the birds were to estimate the increase in metabolic rate above resting conditions. Furthermore, one would like to know the average amount of time spent in each microhabitat. The animals may just be sampling the extreme environments.

In a recent paper Bakken (1979a), using the standard operative environmental temperature, has improved the analysis of Mahoney and King (1977) by incorporating the effects of wind speed reported by Robinson et al. (1976). Bakken found that evaporative cooling in the thermoneutral zone (at low humidities), metabolic rate and overall thermal conductance all appear to be functions of T_e's. Application of laboratory data to field situations are discussed and will be of interest to anyone studying thermal energetics. Figure 7 for instance shows the importance of the bird's physiological state on oxygen consumption.

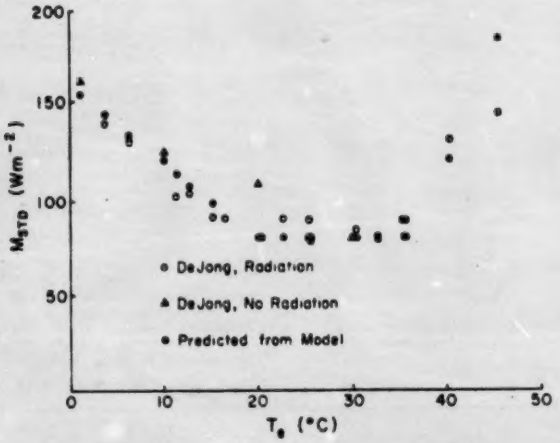

Figure 5. Measured and predicted metabolic rates in relation to equivalent temperature (T_e). Estimates of metabolic rates (M_{std}) are based on each T_e computed from the experimental conditions of DeJong (1976) applied to data on oxygen consumption in white-crowned sparrows reported by King (1964). These predictions (blackened circles) are compared with rates (M_{std}) actually measured by DeJong (1976) without added short-wave radiation (triangles) and with various intensities of short-wave radiation (unblackened circles). (From Mahoney, S.A. and J.R. King 1977, p. 118.)

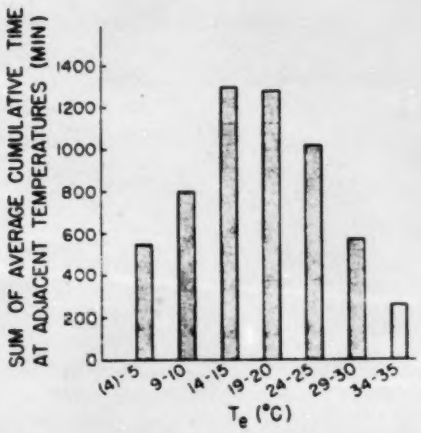

Figure 6. Equivalent temperature preferenda of white-crowned sparrows (mean values for four birds, each tested while alone in the preference apparatus). (From Mahoney, S.A. and J.R. King 1977, p. 199.)

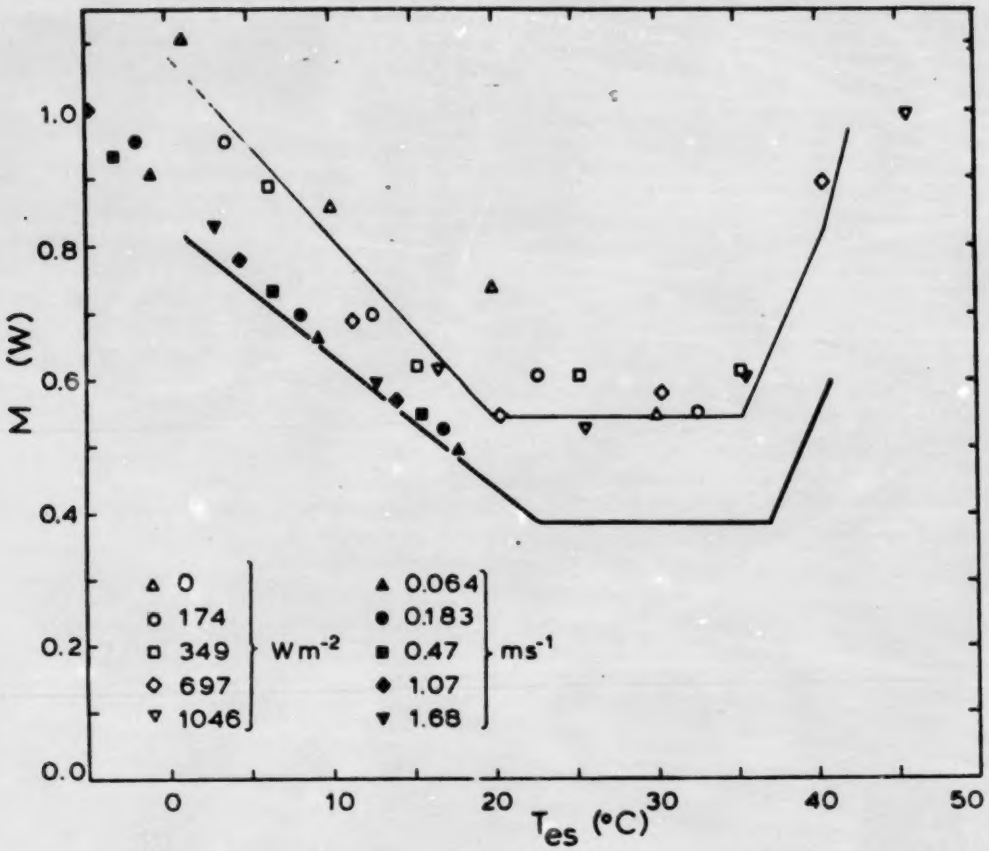

Figure 7. Metabolic rate, M, of white-crowned sparrows, plotted as a function of standard operative temperature, T_{es}, for three different experiments. The solid line is the regression to the data in King (1964). This study used free convection in a darkened chamber. These conditions impose the least physiological stress, and gives the lowest standard metabolic rate in the thermoneutral zone. The birds were summer acclimated, giving a lower critical temperature of about 23°C. The solid symbols are the results of the study of Robinson et al. (1976), which used forced convection in a darkened chamber. Fan noise produces a slight (average of 11%) increase in M over King's (1964) values. Data does not appear to extend into the thermoneutral zone. The open symbols are from DeJong's (1976) study, conducted using free convection in a chamber with various levels of visible radiation. The use of illuminated birds in the active part of their diurnal cycle gives the highest values of M. As these birds are winter-acclimated, the lower critical temperature is around 20°C. Note that the use of standard operative temperature allows the comparison of purely physiological differences under equivalent thermal conditions for different combinations of wind, radiation and air temperature.

A second laboratory application of the T_e concept is given by Bakken (1976b). He has elaborated on the measurement of equilibrium body temperature and thermal conductance of the body. Previously, Newton's law of cooling has been used to describe the change in body temperature (but see Calder 1972, Kleiber 1975).

$$\frac{dT_b}{dt} = \frac{K_n}{C} (T_b - T_a) \tag{7}$$

where

T_b is body temperature (°C),

T_a is air temperature (°C),

K_n is thermal conductance of body tissue (J s^{-1}),

C is the heat capacity of the animal (J),

and t is time (s).

Equation 7 says that the change in body temperature will be zero when the animal's temperature is equal to that of the air. This is not a bad approximation if $T_a = T_e$ and if the metabolic and water loss rates of the animal are small. Bakken (1976a) has shown that a better approximation of the cooling curve is given by

$$\frac{dT_b}{dt} = \frac{K_O}{C} \left(T_b - \left(T_e + \frac{M-E}{K_O}\right)\right) \quad . \tag{8}$$

When $\frac{dT_b}{dt} = 0$,

$$T_b = T_e + \frac{M-E}{K_O} \quad .$$

If the cutaneous water loss is small than equation 8 has the same form as the steady-state equation 6 developed earlier, where

$$T_e = \frac{h_c T_a + Q_n}{h_c + R} \tag{9}$$

and

$$K_0 = \frac{K(h_c + R)}{K + h_c + R} . \tag{10}$$

K_0 is a function of the convection coefficient, h_c, which depends specifically on wind speed; a physical characteristic of the environment. Bakken (1976b) has provided a detailed discussion of the use of equation 7. As an illustration, consider the case when M and E are small (most insects and lizards). Then equation 8 reduces to

$$\frac{dT_b}{dt} = \frac{-K_0}{C} (T_b - T_e) . \tag{11}$$

If wind speed and orientation are constant, the only physiological characteristic of the organism that would make it different from that of an inanimate object is its ability to regulate blood flow. (As an example, see Fig. 8.)

Field Applications

A particularly interesting application of the T_e concept will be in field studies. Bakken and Gates (1975) and Bakken (1976) have reviewed the possibility of making model organisms with the same thermal properties as the animal under study. Using the models, one could map the temporal and spatial variation of the thermal environment. Once the models have been checked in laboratory situations, it will be much easier to take one temperature than to make the many microclimatological measurements necessary to compute the energy budget. Buttemer (1979) is the first to use this method. These measurements include longwave and shortwave radiation, air temperature, wind speed, wind direction and relative humidity. With this

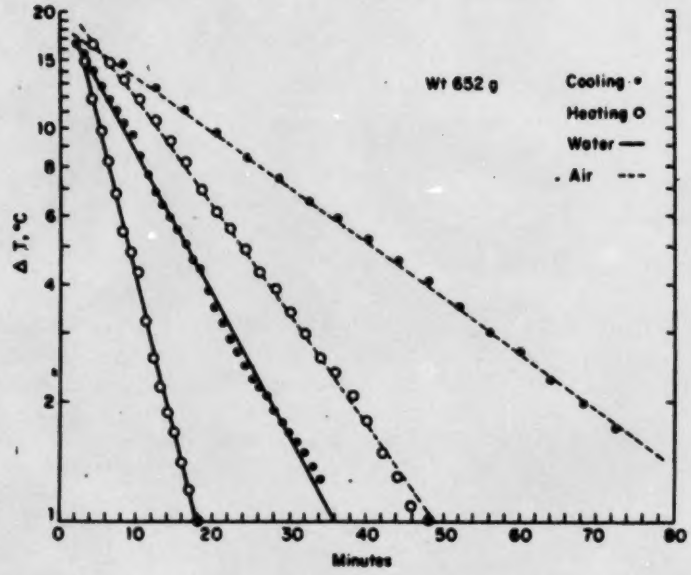

Figure 8. Heating and cooling rates of the Galápagos marine iguana (Amblyrhynchus cristatus) in water and air. ΔT is the difference between body and ambient temperatures (T_a). During heating T_a=40°C; during cooling T_a=20°C. (From G.A. Bartholomew and R.C. Lasiewski, 1965, Comp. Biochem. Physiol. 16:573-582.)

map in hand, it will be easy to see if the animal is selective in how it uses the environment. For example, one could ask, "Is the laboratory behavior found in the sparrows studied by Mahoney and King (1977) exhibited out of doors?" The T_e concept is a straightforward method for tackling this kind of problem.

What would such a map look like? Data presented by Bakken and Gates (1975) in Table 2 gives some insight. The authors investigated the effect of absorptivity (points 1-3), orientation (3-5), microhabitat (3, 6-8) and size (9-13).

This approach will allow one to answer the question of whether or not animals avoid stressful environments. And what proportion of their time is spent in nonequilibrium, requiring the organism to monitor its heating and cooling rates. Operative environmental temperature distributions combined with physiological measures of animals in the natural environment will give a better understanding of the influences of the thermal environment. An interesting example of such measurements is the body temperature telemetry taken from Pearson and Bradford (1976), who studied the thermoregulation of the lizard Liolaemus multicarpus and the toad Bufo spinulosus high in the Andes mountains. Figure 9 shows a record of the body temperature of both animals as a function of time. Although in similar microhabitats, each species interacts with the environment quite differently, which is manifested in their different body temperatures and activity patterns.

SUMMARY

In this module, we have reviewed some of the historical developments in the study of animal thermoregulation. Besides trying to relate the

Cylinder	Diameter (cm)	Position	Exposure	Height (cm)	Color	T_c (°C)
1	1.6	ESE-WNW	Sun	0.3	White	37.5
2	1.6	ESE-WNW	Sun	0.3	Black	50.0
3	1.6	ESE-WNW	Sun	0.3	Gray	45.5
4	1.6	NNE-SSW	Sun	0.3	Gray	46.0
5	1.6	Vertical	Sun	0.3	Gray	41.0
6	1.6	ESE-WNW	Sun	20.0	Gray	39.5
7	1.6	ESE-WNW	Sun	90.0	Gray	36.0
8	1.6	ESE-WNW	Shade	1.0	Gray	28.3
9	0.64	ESE-WNW	Sun	0.3	Gray	41.5
10	1.6	ESE-WNW	Sun	0.3	Gray	45.5
11	2.86	ESE-WNW	Sun	0.3	Gray	45.5
12	3.81	ESE-WNW	Sun	0.3	Gray	47.5
13	15.50	ESE-WNW	Sun	1.0	Gray	47.0

Table 2. A small shrub 0.5 m high provided broken shade for cylinder 8. All cylinders were in an area of 1 x 2 m. Microclimate parameters for this area were as follows: T_{air}=26°C, T_{ground}=38.5°C; wind at 20 cm, 67 cm s^{-1}; wind at 90 cm, 310 cm s^{-1}; solar radiation in an 0.3- to 3-μ band, 1.3 cal cm^{-2} min^{-1}. August 17, 1972, 14:15 to 14:16. Douglas Lake, Cheboygan County, Michigan. (From Bakken, G.A. and D.M. Gates 1975, p. 265.)

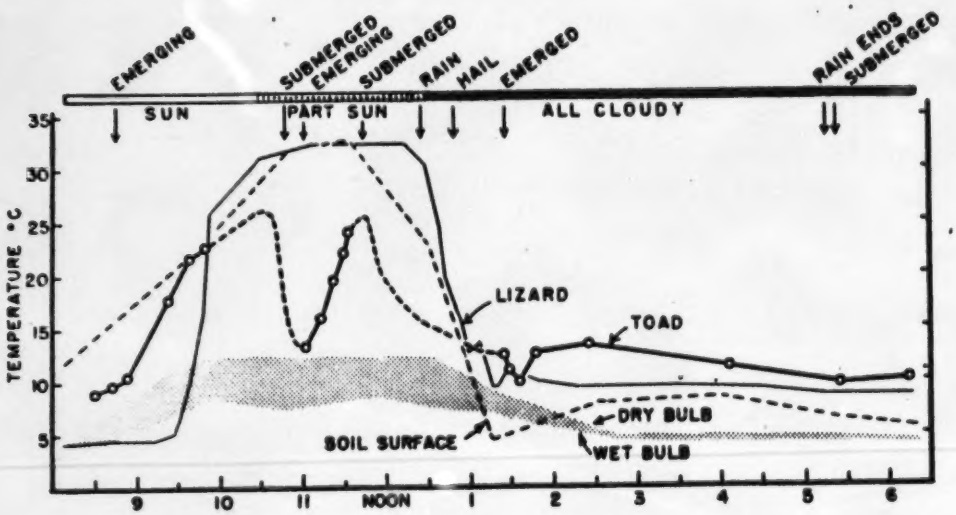

Figure 9. Body temperature of a telemetered free-ranging Bufo spinulosus compared with that of a telemetered free-ranging Liolaemus multiformis at the same time. 22 March; 4,300 m. Temperature of soil surface was measured at a spot exposed to the sun. Comments at top of the figure referring to submergence and emergence pertain to the toad. (From Pearson, O.P. and Bradford, D.F. 1976, p. 165).

discussion to other ecological areas, especially foraging, I have endeavored to point where a quantitative knowledge of the heat transfer processes has helped to clarify the adaptive significance of animal morphology, behavior and physiology. Bakken and Gates (1975), Campbell (1977) and others (see Bakken 1979a for review) have developed the operative environmental temperature as a way to summarize how the organism "feels" the thermal environment. This concept will have useful applications in both physiology and ecology.

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PROBLEMS

1. Pick an animal and discuss what factors in Table 1 will be most important in its thermoregulation strategy. Include in your response any factors that have been omitted from the table.
2. When an endothermic animal is resting, there can be a range of standard operative environmental temperatures within which its heat production or metabolic rate is constant. This thermal neutral zone, as it is called, is shown in Figs. 1a, 5 and 7. What mechanisms does an animal have available to maintain constant core temperature and heat production when the thermal environment is changing? Discuss the relative importance of each.
3. a) Using the information in Fig. 2, what are the avenues of heat gain and heat loss for an exercising rabbit?

   b) At different temperatures, some terms are constant while others are changing. Why? Identify the factors which may have caused the end of the exercise period. Is there a temperature at which one of these factors is likely to be more important?
4. Appendages serve a variety of functions but all are included under Allen's rule. Contrast the foot of a seagull with its wing with regard to the importance of each for heat balance when the animal is resting and exercising. (You may choose your own organism and set of appendages.) Support your discussion with knowledge about other functions of the appendages. Any physiological or behavioral information will strengthen your conclusions.
5. You are researching the prospects of entering the aquaculture business raising sockeye salmon (Oncorhynchus nerka). In the graph below juvenile

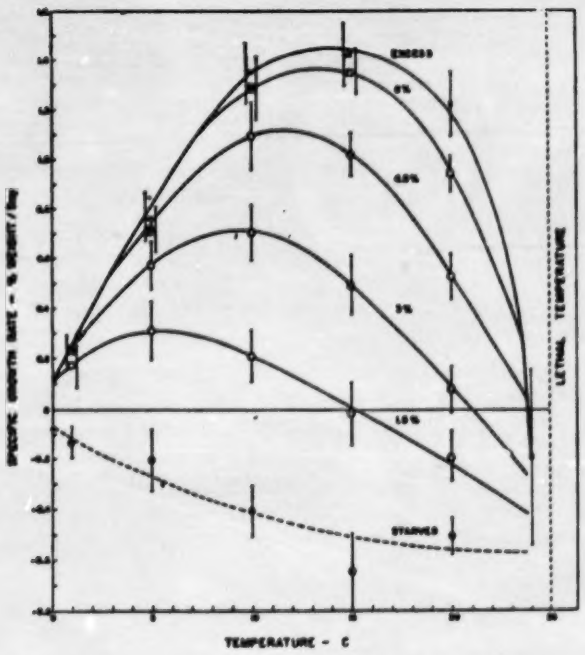

Figure 10. Effect of reduced ration on the relation between growth rate (±2 SE) and temperature, for 7- to 12-month-old sockeye. Points for excess ration or where a prescribed ration turned out to be excessive are marked with an X. The broken line for starved fish is a provisional interpretation. (From Brett, J.R. et al. 1969, p. 238.)

sockeye growth is given as a function of food and temperature conditions. What is the temperature for maximum growth rate when food rations are at 6, 4.5, 3.0 and 1.5% of dry body weight per day. Fish food is relatively cheap and you could afford to provide maximum rations, but the average water temperature in the pond you plan to use is only 7 C so that the fish are not achieving maximum growth rates. Discuss the conditions in which it would be economically advantageous for you to raise the water temperature. How high would you raise it? What might be the ecological consequences of heating the water for the rest of the aquatic community.

6. Imagine that you are studying the foraging and activity patterns of the Ortax, a large ungulate, and a carnivorous beetle, the Diplitz. You have divided the day into ten equal time periods and measured F_x, M_{fx}, and M_r for each period as shown in the table below.

Time Period	Ortax			Diplitz		
	F_x	M_{fx}	M_{rx}	F_x	M_{fx}	M_{rx}
1	6	3	2	20	10	1
2	6	5	2	25	10	2
3	7	7	3	8	10	2
4	7	2	3	4	10	2
5	7	2	2	2	10	2
6	7	2	1	0	9	2
7	8	1	1	1	9	1
8	6	2	2	2	8	1
9	6	4	2	7	7	1
10	6	2	1	14	8	1

Rank the time periods in order of decreasing net caloric profit, assuming the animals can choose between resting and foraging. Are there any time periods the animals should be resting instead of feeding? If both organisms are tyring to gather energy stores, what pattern of feeding activity would you expect to see using this simple model? What is the

most each can expect to "make" during one cycle? If the Ortax must make a net profit of 20 caloric units per day to prepare for winter when should it feed to minimize total feeding time? If it must maintain weight how should it feed? If both animals must wait one time period to digest its food after it has a full stomach of 22 units, what is its feeding schedule to maximize net profit? Remember to consider F_x values to figure digestion limits. Assume the Ortax must skip two periods. How should it feed to maximize profit?

7. You work as a biologist for the consulting company Envirotech. The firm's latest contract calls for an evaluation of the potential impact on the quail populations of a logging plan, Americana National Forest. Describe how you would fulfill this contract. Specifically, discuss the importance of food and cover on population densities and individual health.
8. Using the theory derived in the module and the data below, calculate T_b for the three cases given. What is the environmental and the physiological contribution to T_b in each case? What two finds of animals are represented?

TABLE OF VARIABLES

Animal	M ($W\ m^{-2}$)	E_r ($W\ m^{-2}$)	E_b ($W\ m^{-2}$)	Q_a ($W\ m^{-2}$)	K ($W\ m^{-2}°C^{-1}$)	T_a (°C)	M_b (kg)
1	20	--	10	550	180	15	0.07
2	150	25	100	750	15	20	0.008
3	45	--	40	850	200	25	0.010

Assume ε=0.95, V=0.25 m s^{-1} $\bar{T}_r$=25°C, h_c=17.24 $V^{0.60}$ $M_b^{-0.133}$.

9. Using the data in problem 8 for the two ectotherms, calculate k_o for $V = 0.1$, 0.5, and 3.0 m s^{-1}. Assume that the difference between metabolism and water loss is zero. What is T_b in each case now? If the heat capacity is equal to the specific heat (3430 J kg^{-1} $°C^{-1}$) times the mass of the animal, what is the heat capacity for each? Assuming $Q_a = 600$ W m^{-2} and $T_a = 20°C$ for the range of wind speeds above which animal will get warmer. Are your conclusions still the same if $Q_a = 380$ W m^{-2}? Integrate equation 11 to find T_b as a function of time. If the initial body temperature of both animals is 10 C at time equal to zero, which animal will get to $T_b = 25°C$ first? Use the following relationship from Mitchell (1976).

$$\text{Area} = 11.0 \times \left(\frac{\text{body mass}}{\text{body density}}\right)^{2/3},$$

where body density equals 1×10^3 kg m^{-3} to correct the dimensions of the equations. What is the difference in time between when each will arrive at 25°C? (Hint: Solve the integrated equation for time.) Answer the preceding two questions for V=.1 and .5 m s^{-1}. Assume the animals are lizards and comment on Cowles' suggestion.

10. Include a conduction term of the form $G(T_r - T_g)$ in equation 3 and find an equation analogous to equation 6 for T_b.

11. Imagine you are employed as an entomologist with the U.S.D.A. working with a team of research scientists studying a pest that drills into the stalks of corn. Your assignment is to investigate the importance of the physical environment in the corn-insect interaction. Ten years of historical data suggest that during cold springs the corn is not badly infected. Also it is known that chemical treatments are most effective

on the third instar. These specific questions are important to managing this pest.

a) Will this be a high density year for the corn drill so that biological or chemical controls will be needed?

b) If so, when during the season will most of the insects be in this instar? Discuss your research plan to address these questions.

PROBLEM SOLUTIONS

1. As a sample answer, consider the response of the bumblebee to its thermal environment. At northern latitudes these bees are active for only a small portion of the year when food and the thermal environment are favorable. Temporal partitioning of the environment is also important on a daily time scale. During inclement weather, the workers stop foraging. The general importance of habitat selection and of body orientation are unknown. Heinrich (1976) has discussed the important role of the circulation system used to maintain thermal equilibrium during flight in the bumblebee. Certainly the hairy outer coat of these animals is important in heat exchange and at higher temperatures the animals can evaporate water.

2. The animal can change its blood flow rates, circulation patterns, water loss, orientation and posture to maintain a constant body while the thermal environment is changing but its body temperature and metabolic rate are constant. The relative importance of orientation and posture is unknown. Figure 1b of the module indicates that the compounded effect of blood flow and circulation patterns are important in the lower part of the thermal neutral zone while evaporative water loss becomes more important at higher environmental temperatures.

3. a) Anaerobic and aerobic metabolism produce heat. (The rabbit will also absorb radiation from the environment but this is represented as R where R=radiation absorbed-radiation emitted.) The animal loses heat via evaporation, convection and radiation exchange. Conduction is assumed to be zero.

b) The heat production terms are constant as a function of temperature because these terms are associated with the energy needed for movement. Evaporative water loss is approximately the same for the temperature range loss which in turn is a function of O_2 consumption. O_2 consumption is constant; therefore we expect respiratory losses are constant. The sum of dry heat loss (convection and reradiation) and storage are relatively constant, buy as heat loss terms increase at colder ambient temperatures, the storage term decreases. When air temperature drops more heat can be lost to the environment because the difference between the surface temperature and the ambient temperature is larger. The exercise period may have ended because of lactic acid build-up due to anaerobic metabolism or because of an increase in body temperature. The first factor is independent of temperature while overheating is more likely at higher temperatures.

4. Appendages fall into at least three categories. A rabbit's ear can be used to increase heat loss by increasing blood flow to this appendage if the environmental temperature is below core temperature. In contrast, many limbs are used during movement and then the overriding concern becomes supplying blood to the muscles. Under these conditions, the appendage cannot be used to regulate heat balance. This is not to say that the appendage cannot show thermoregulatory adaptations. For example, consider the well-known counter current system of blood vessels and arteries in dolphin flippers which reduce heat loss. A third group of appendages requires careful regulation (head, scrotum, mammary groups). The heat may have steep temperature gradients from the nose to the brain but brain temperature is carefully regulated. Likewise, to maintain

viable sperm the temperature of any male reproductive organ is carefully controlled.

To answer the question specifically posed, gulls have been shown to use their feet as heat radiators during flight (Baudinette et al. 1976). In cold arctic climates when the bird is placed on ice, blood flow is increased to foot to keep it from freezing (Scholander and Schevill 1955). When resting the wings will add insulation to the body. During flight extension of the wings greatly increases surface area, but because there is little muscle mass in the wings. The ability of the bird to use its wings for temperature regulation is unknown.

5. The temperatures for maximum growth with food rations at 1.5, 3.0, 4.5 and 6.0% of dry body weight are 5, 9, 11.5 and 13.5°C, respectively. The conditions necessary to increase water temperature from a economic standpoint can be stated in a verbal model as profit equals fish price minus food costs minus heating costs. Because food production, maximum food ration and heating costs will all increase as water temperature increases, it is difficult to say how high water temperature should be increased for maximum profit--certainly not above a water temperature of 13.5°C. The ecological consequences for heating the water are difficult to predict, although mush has been written. It is important to remember that both the chemical and physical properties of the water will change.

6. ORTAX

Time Period	F_x	$F_x - M_{fx}$	Ranking	M_{rx}	Ranking	$F_x - M_{fx} - M_{rx}$	Ranking
1	6	3	6.5	1	2.5	4	8
2	6	2	8.5	2	6.5	4	8
3	7	0	10	3	9.5	3	10
4	7	5	3	3	9.5	8	1.5
5	7	5	3	2	6.5	7	3
6	7	5	3	1	2.5	6	4
7	8	7	1	1	2.5	8	1.5
8	6	3	6.5	2	6.5	5	5.5
9	6	2	8.5	2	6.5	4	8
10	6	4	5	1	2.5	5	5.5
Σ		36		18			

DIPLITZ

Time Period	F_x	$F_x - M_{fx}$	Ranking	M_{rx}	Ranking	$F_x - M_{fx} - M_{rx}$	Ranking
1	20	10	2	1	3	11	2
2	25	15	1	2	8	17	1
3	8	-2	5	2	8	0	5
4	4	-6	6.5	2	8	-4	6
5	2	-8	8.5	2	8	-6	8
6	0	-9	10	2	8	-7	9.5
7	1	-8	8.5	1	3	-7	9.5
8	2	-6	6.5	1	3	-5	7
9	7	0	4	1	3	-1	4
10	14	6	3	1	3	7	3
		31		15			

The Ortax should always feed to maximize net energy gain. The Diplitz should not forage in time periods 4-8. Their net profits are 36 and 23 respectively. To minimize feeding time and still make a net profit of 20 units, the Ortax should feed in time periods 7, 4, 5, 6, 10 and 8. Feeding should take place in periods 7, 4 and part of 5 if the animal must simply maintain weight.

The Ortax should not feed during periods 3.5 and 9 for a net profit of 25 (29-4) when one period is required for digestion. The Diplitz should forage during periods 9 and 10 and part of period 2 for a net profit of approximately 9 units. If two periods are required for digestion, then the Ortax will feed in periods 10, 1, 2, 5.6 and most of period 7 for a net profit of 10.

7. Wildlife biologists including Stoddard (1931), Errington (1967) and Leopold (1977) have summarized much of the work on quail populations in different kind of environments throughout the United States. In general logging will open up the forest producing successional vegetation which can provide abundant food supplies as well as the necessary shelter. Thus one would expect densities of quail to increase for 10 to 35 years and then slowly drop off as the forest canopy developed.

8. $R = 5.71\ W\ m^{-2}\ k^{-1}$

Animal	h_c $W\ m^{-2}\ °C^{-1}$	Q_n $W\ m^{-2}$	T_e °C	Physiological Contribution °C	T_b °C
1	10.65	1827.10	26.11	.67	27.78
2	14.28	2027.10	37.67	4.58	42.45
3	13.86	2127.10	46.70	.28	46.98

Animals 1 and 3 are ectotherms because M and E are small while animal 2 is an endotherm.

9. From problem 8: $\bar{T}_r = 25°C$

$R = 5.71\ W\ m^{-2}\ °C^{-1}$,

$3\sigma\epsilon\ \bar{T}_r^{\,4} = 1277.1\ W\ m^{-2}$,

$h_c = 17.24\ V^{0.6}\ M_b^{-0.1333}$,

Animal	K_o $W\ m^{-2}\ °C^{-1}$	M_b kg	C $J\ °C^{-1}$	A m^2	C/A $J\ °C^{-1}\ m^{-2}$
1	180	0.07	240.1	0.01868	12853
3	200	0.01	34.3	0.005106	6718

Body temperature will equal the operative environmental temperature.

Parameter	Animal	V ($m\ s^{-1}$) .1	.5	3.0
h_c ($W\ m^{-2}\ °C^{-1}$)	1	6.17	16.21	47.51
	3	8.00	21.02	61.59
K_o ($m^2\ °C\ W^{-1}$)	1	11.147	19.543	41.068
	3	12.832	23.579	50.352
T_b (°C) for Q_a=600 $W\ m^{-2}$	1	37.10	29.27	23.83
	3	34.82	27.60	23.02
T_b (°C) for Q_a=380 $W\ m^{-2}$	1	18.58	--	--
	3	18.77	--	--
$\frac{C}{K_o A}$ (s)	1	1153.043	653.68	312.97
	3	523.53	284.910	133.42
Time to reach 25°C (s)	1	929.73	985.05	
	3	485.43	544.85	
Difference		444.30	440.20	

10. $Q_a + K(T_b-T_r) = Q_e + C + E_r + G(T_r-T_g)$ (1)

$M = E_b + K(T_b-T_r)$ (2)

$Q_a + K(T_b-T_r) = RT_r - 3\sigma\epsilon\bar{T}_r^4 + h_c(T_r-T_a) + E_r + G(T_r-T_g)$

$Q_n + K(T_b-T_r) = RT_r + h_c(T_r-T_a) + E_r + G(T_r-T_g)$

$T_b - \left(\frac{M-E_b}{K}\right) = T_r$

$Q_n + M - E_b - E_r = RT_r + h_cT_r - h_cT_a + GT_r - GT_g$

$Q_n + h_cT_a + GT_g + M - E_b - E_r = [R + h_c + G]T_r$

$$T_b = \frac{Q_n + h_cT_a + GT_g + M - E_b - E_r}{R + h_c + G} + \frac{M - E_b}{K}$$

$$= \frac{Q_n + h_cT_a + GT_g}{R + h_c + G} + \frac{KM - KE_b - KE_r}{K(R+h_c+G)} \quad \frac{(R+h_c+G)(M-E_b)}{K(R+h_c+G)}$$

$$T_b = \frac{Q_n + h_cT_a + GT_g}{R + h_c + G} + (M-E_b)\frac{K + R + h_c + G}{K(R+h_c+G)} + \frac{E_r}{R + h_c + G}$$

11. a) Many ecological factors will be important in determining the sucess of the corn drill in any particular spring. Over-wintering density of the pest, predator densities and parasite densities may be necessary variables to include in a predictive equation. Laboratory facilities which can reproduce the climate that the animals experience in field will help define the physiological limits that the insect can tolerate. Statistical models might be employed to provide survival estimates based on microclimate variables.

b) During the spring a similar approach as described above will help determine when the third instar will occur given the history of the

climate that spring. Then appropriate control actions could be initiated to consider the physiological state of the host plant because this will influence the quality of the food that the pest is getting. Certain weather patterns might favor a strong plant defense response lowering the tissue nutritional quality. Depending on how the insect responds to the same weather patterns the net effect may be an increase or a decrease in survival rates. Simultaneous field work documenting survival and development rates as a function of climate would be important complementary research.

APPENDIX I. OPERATIVE ENVIRONMENTAL TEMPERATURE

Symbols, Units and Dimensions

Symbol	Quantity	Unit	Dimension	S.I. Equivalent
A	Area	m^2	L^2	---
C	Convection	$W\ m^{-2}$	$HL^{-2}T^{-1}$	---
C	Heat capacity	$J\ °C^{-1}$	$H\theta^{-1}$	---
E_b	Body water losses	$W\ m^{-2}$	$HL^{-2}T^{-1}$	---
E_r	Surface water loss	$W\ m^{-2}$	$HL^{-2}T^{-1}$	---
e_x	Net energy gained in period x	W	HT^{-1}	---
F_x	Food captured in period x	W	HT^{-1}	---
G	Conduction coefficient	$W\ m^{-2}\ °C^{-1}$	$HL^{-2}T^{-1}\theta^{-1}$	---
h_c	Convection coefficient	$W\ m^{-2}\ °C^{-1}$	$HL^{-2}T^{-1}\theta^{-1}$	---
K	Conductivity of body	$W\ m^{-2}\ °C^{-1}$	$HL^{-2}T^{-1}\theta^{-1}$	---
K_O	Conductance	$W\ m^{-2}\ °C^{-1}$	$HL^{-2}T^{-1}\theta^{-1}$	---
K_n	Conductance	$W\ m^{-2}\ °C^{-1}$	$HL^{-2}T^{-1}\theta^{-1}$	---
M	Metabolic rate	$W\ m^{-2}$	$HL^{-2}T^{-1}$	---
M_b	Body mass	kg	M	---
M_{fx}	Metabolic cost of foraging in period x	W	HT^{-1}	---
M_{rx}	Metabolic rate while resting in period x	W	HT^{-1}	---
Q_a	Absorbed radiation	$W\ m^{-2}$	$HL^{-2}T^{-1}$	---
Q_e	Emitted radiation	$W\ m^{-2}$	$HL^{-2}T^{-1}$	---
Q_n	Radiation factor	$W\ m^{-2}$	$HL^{-2}T^{-1}$	---
R	Radiation conductance	$W\ m^{-2}\ K^{-1}$	$HL^{-2}T^{-1}\theta^{-1}$	---
T_a	Air temperature	°C	θ	---
T_b	Body temperature	°C	θ	---
T_e	Operative environmental temperature	°C	θ	---
T_g	Ground temperature	°C	θ	---
T_r	Surface temperature	°C	θ	---

c1

c2

APPENDIX I (cont.)

Symbol	Quantity	Unit	Dimension	S.I. Equivalent
t	Time	s	T	---
V	Wind velocity	$m\ s^{-1}$	MT^{-1}	---
W_x	Metabolic cost of waiting through period x	W	HT^{-1}	---
ε	Emissivity	---	---	---
σ	Stefan-Boltzmann constant 5.67×10^{-8}	$W\ m^{-2}K^{-4}$	$HL^{-2}T^{-1}\theta^{-4}$	---

M = mass
T = time
L = length
θ = temperature
$H = ML^2T^{-2}$